in spirit they at once seize one another and form themselves up into a complete mass, which is tightly held together by the mandibles.

The "soldier" of *Atta cephalotes* is the same in form in Nicaragua as in Trinidad, and possesses the same powers of defence and offence.

Trinidad,
January 9, 1896.

XXIV.—*The Sense of Sight: Sketch of a new Theory.*

By H. M. Bernard, M.A. Cantab., F.L.S., F.Z.S.

For nearly ten years I have been engaged in endeavouring to find an explanation of light sensations. I have at last worked out a theory capable of connecting and explaining most of the phenomena, and, what is still more important, apparently capable of demonstration. I am now engaged in arranging the evidence; but in the meantime I am urged to publish a short abstract of the conclusions arrived at, because, in the first place, the duties which I have undertaken at the Natural History Museum must necessarily retard the publication of a fuller treatise, and, in the second place, because, the subject being one of wide interest, physiologists and zoologists will have an opportunity of recording observations either for or against the theory, which will be useful towards the ultimate solution of this important problem.

In the following pages I propose to confine myself solely to a statement of my own theory, abstaining entirely from all criticism, and even from all mention of existing theories, except when the subject requires it.

A long series of observations on different Metazoa, ranging from the Platodes to the Vertebrates *, have convinced me not only that wandering-cells, apparently acting as scavengers among the tissues, collect granules discharged from other cells or matter to be afterwards formed into granules, but that the importance of this process is not exclusively physiological. These granules are conveyed by the wandering-cells to organs which lead out of the body, where they may be put to secondary uses. The granules themselves not only differ greatly in different animals, but may also differ in one and the same animal. The secondary utilization of these granules takes place, in many cases at least, by their transference from

* Not including, however, the Echinoderms; and on these *cf.* Mr. H. Durham's paper in the 'Quarterly Journal of Microscopical Science,' vol. xxxiii. p. 81.

the wandering-cells into those of other tissues to which they have been brought. Just as the cells of the tissue where they originated passed them on to the wandering-cells, these can again pass them on to other cells. I may, perhaps, recall the collections of pigment-cells within the ovaries of frogs, which appear to be passing their coloured granules into the eggs.

Chief among the tissues receiving the loads brought to them by the wandering-cells is the outer skin. Here they can be seen discharging their granules to the epidermal cells, which utilize them in various ways. They take part—probably a very important part—in the formation of epidermal protective structures, chitinous and horny cuticles, &c. Slime-glands appear to use them in the formation of their secretions. Or, again, they are stored up, altered or unaltered, as the colouring-matters of the skin and of its derivatives.

Remarkable among skins coloured by these granules are those endowed with what is known as the chromatic function. In these cases the wandering-cells have either been arrested in the connective tissue just beneath the skin, or have given up their granules to connective-tissue cells, the resultant "chromatophores" coming under partial control of the nervous system. The highest specialization of this is seen when, in two or more layers of cells containing differently coloured granules, these granules change their positions in the bodies of the cells, spreading out or crowding together at different times and in different degrees, so as to produce an astonishing play of colour. But even in such cases it is probable that individual granules escape from these secondary detentions and reach the outer cells of the skin, where they may be needed for various more primary functions.

Leaving out of account those cases which are complicated by secondary association with the nervous system, we have abundant evidence to show that, although the wandering-cells under discussion somehow travel to their respective destinations in the dark, they are very sensitive to light, towards the source of which they move. This is a common phenomenon among unicellular organisms both animal and vegetable, and it is specially marked when the contents of the cells are coloured. It is in large measure to this attraction that the great abundance of the granule-bearing cells or of transported granules in or under the skin is due.

The theory which I desire to propound is, that it is to this constant striving of wandering-cells to travel towards the light, and, if possible, to escape altogether from the cell-complex of the body in which they originated (or, perhaps, only to discharge their contents at the surface), that the animal kingdom owes its many visual organs. It is legitimate to assume that the laden wandering-cells would flock in excess towards the source of the brightest light. At such points complications would arise between these invaders and the more stationary tissues which bar the way. Out of such complications, I believe, eyes have arisen. The sensory nerves in those parts of the skin most strongly and frequently illuminated become associated in different ways with these complications, either with the struggling crowd of wandering-cells collected in excess at such bright spots, and set in commotion whenever light falls on them, or with other cells into which these wandering-cells have discharged their contents to overcrowding, and which, on this account, practically become equally restive whenever subjected to light-stimulus. For it is important to note that these granules appear to make the same endeavours under light-stimulus to leave the cells in which they find themselves and travel towards the light, as do the wandering-cells themselves to escape from the Metazoan body.

We may enumerate some of the different types of eye which can be thus accounted for.

1. Simple epidermal cells associated with epithelial sensory (tactile) cells become filled with granules to overcrowding. The escape of these granules at the exterior is hindered by the excess of slime to which they themselves have contributed. These granules, crowding forward whenever stimulated by light, but unable to escape fast enough, exert a lateral pressure upon the adjacent sensory cells. The excess of slime produced by the continual crowding forward of the granules may result in the formation of vitreous bodies or lenses. Eyes arising in this way occur, for instance, in some Mollusks.

2. The wandering-cells may be arrested by, or collect in excess round, epithelial glands which have sunk below the surface. This would be especially the case round gland-cells or glands which contained glassy or refractive contents in the line of light, such bright points having, according to the theory, an especial attraction for the wandering-cells. The striving of the wandering-cells either to push on through, or to pass on their contents to, these cells would again be appreciated by sensory nerves. Further, assuming, and there is ground for the assumption, that the granules in many cases contribute to the formation of the slimy or refractive secretions in such glands, these secretions would, owing to the excessive supply of granules, tend to develop abnormally, and thus help to form a more efficient dioptric apparatus than the simple gland

afforded. The eyes in certain Platodes, and apparently also in Leeches, are essentially of this type.

3. In cases where a rigid chitinous cuticle is present, the different ways in which the cells containing the granules become associated with the sensory nerves are very numerous. These cells may belong either to the skin or to the connective tissue, or are, perhaps, collections of the wandering-cells themselves. Leaving these differences on one side, we may roughly divide the eyes arising under chitinous cuticles into two groups—those in which the sensory nerves running close under the cuticle turn round and face the advancing crowds of granule-bearing cells or granules, and the other in which the sensory nerves run with the stream towards the light. In both these divisions we have many specializations of the different cells composing the ultimate complex or organ, while in all cases the excess of the advancing granules, which normally contribute an important constituent to the hard cuticle, leads to the formation of rods, rhabdomeres, crystalline cones, and lenses. We have, then, here to assume that individual granules, though evidently impeded by the structure of the complex, continually succeed in their efforts to advance and in some way end by fulfilling their normal destiny of helping to build up chitin.

The secondary character of visual organs seems to follow from the fact that eyes showing both the positions of the sensory (retinal) cells described under this heading occur in one and the same animal class, *e. g.* in the Arachnida and in the Mollusca.

Before passing on to the typical complicated vertebrate eye I may refer to the persistent remains of a far simpler kind of eye which are still to be found among lower vertebrates. I refer to the ancient pineal eye, which is still recognizable as an eye in the Lizards. This pineal eye, if its present condition, say in *Hatteria*, gives any evidence of its original morphology, and it would be difficult to prove the contrary, is of the first and simplest of the types above described *, and thus morphologically, as well as phylogenetically, is a very primitive structure. The pigment-granules or granule-bearing cells which, in the functional eyes of that type, contribute to the formation of the cuticular or gelatinous dioptric apparatus, in

* I have to thank my friend, Mr. Martin Woodward, of the Royal College of Science, for the loan of sections of the pineal eye of *Hatteria*, which leave no doubt in my mind on this point. I may add that I am greatly indebted to other fine preparations made and kindly lent me by Mr. Woodward; they have confirmed in a striking manner many points in my theory.

these degenerate eyes appear usually to escape into the cavity of the eye, in some cases at least, unaltered *.

Turning to the vertebrate eye proper, we are justified in affirming that, however highly specialized, it is a product of the same activities as have given rise to the simpler eyes above described. With regard to its structure, what chiefly concerns us is the fact that the sensory cells are turned towards the advancing streams of granules. I feel justified in speaking of the streams of granules, because, as is known, not only are these granules carried about in cells, but they are apparently capable, under the action of stimulus, of independent movements within cells, and, further, can pass from cell to cell. Amœboid movements have been claimed for the individual granules from the eye of vertebrates when floating free in a suitable medium. That the granules in many eyes are highly complex bodies (perhaps secondarily specialized), and not simple concretions, follows from the fact that they seem to contain a staining kernel of chromatin, and in the eye of the crustacean *Apus* they are invested in a fine hyaline layer of matter and can be found dividing †.

Passing by cornea, iris, lens, and other accessory structures, we may say that the vertebrate eye, as a sense-organ, consists essentially of a thick layer of nerve and sensory tissue effectually opposing, or only greatly impeding, the advance of granules contained in the cells of an epithelium which is in contact with this sensory layer over its whole extent. These granules should normally reach the surface of the body and take part in the formation of the external protective structures. They are, however, kept back, but are stimulated to renewed efforts every time the light falls on them. This attack on the nervous-tissue layer, to try and force a way through whenever attracted by the light, I believe to be the secret of our light sensations.

We may point out here that albinism, which has hitherto prevented physiologists from seeing in the movements of the pigmented granules any essential factor in the production of light sensation, is no difficulty to this theory ‡. The granules themselves are doubtless there in some form or other, only they lack the colour. This deficiency may be quantitative or

* *Cf.* W. Baldwin Spencer, "On the Presence and Structure of the Pineal Eye of the Lacertilians" (Q. J. M. S. xxvii. 1887).

† In conjunction with the normal granules others of such purely excretory matter as guanin are found in some eyes. This phenomenon is quite in accordance with our theory.

‡ The seductive analogy between the eye and a photographic camera with its sensitive films has also had something to do with drawing a tention away from the pigmented granules.

merely qualitative *. That these granules, in spite of this deficiency, seek the light, we gather from the fact that the outer skin of albinos is, but for the absence of colour, apparently normal. The connexion between the granules and integumentary protective structures has already been referred to, and need not here be repeated. I may merely remark that we have almost every gradation between dark-skinned people with coal-black eyes, through fair-skinned people with less deeply pigmented eyes, to albinos with so little pigment in their skins and eyes that, if present at all, it is not at first sight apparent. Perhaps faint traces might be found if the granules of the eyes were specially examined for that purpose. My own, all too limited, observations on this point have so far left me undecided.

We may conclude, however, that the colour of the granules is not essential, for, without it, they strive to reach, and in the skin succeed in reaching, the surface. Nevertheless the fact that the granules collected in visual organs are, as a rule, deeply coloured, shows that the colour is very useful. Its absorption of the light prevents a diffusion injurious to clear vision, and, perhaps, also increases the vigour of the movements of the granule by slightly raising its temperature.

We have, then, these two tissues to consider :—

(1) The layer of cells (choroidal or pigment epithelium) containing the usually pigmented granules, which seek to force a way towards the source of the light that stimulates them to action.

(2) The thick layer of tissue, chiefly nervous and sensory, which blocks the way, *i. e.* the retina.

We will, for convenience, take the latter first.

The Retina.—It will be freely admitted that it is not easy to give a simple morphological definition or description of this complicated structure. While certain of its elements are fairly well understood, we are still far from a complete comprehension of it as a whole. In fact, the application of the most recent and approved methods of staining tend, it seems to me, to make it more enigmatical than ever. What follows is therefore put forward purely tentatively. The retina is a many-layered sensory epithelium, in which originally, *i. e.* when less highly developed, the cells stretched as fine thread-like strands between its limiting membranes, the nuclei being suspended on these threads at different levels. This is a

* Pigmented granules lose their colour in the process of being transformed into cuticle or slime within epidermal cells. This fact largely explains why the two have not hitherto been associated in the manner suggested above.

common type of sensory epithelium, and, as far as the retina is concerned, describes fairly well the undifferentiated portion of that structure as seen in the eyes of tadpoles round the rim of the retinal cup, although the layers of nuclei are even here already numerous. For some little distance round the outside of this rim the granule-bearing cells of the choroidal epithelium are in close contact with the external limiting membrane of the retina—that is to say, there are no rods or cones keeping them at a distance. As we go further from the rim these begin to appear, and the manner of their appearance seems to me to be very significant.

What first strikes one is that they are far less numerous than the nuclei, which at this point have still further increased in number without any very marked signs of differentiation among them. So many nerve-cells with so few terminal structures involuntarily suggest that these end-structures, the "rods and cones," must contain many separate nerve-fibrils. This suggestion finds support in the irregular thickness of the rods and cones. Some receive far more nerve-fibrils than others. There would thus be no morphological difference between these structures, *i. e.* between rods and cones, whatever difference there might be among them as to length or thickness. The rod-like structures, however, are not composed wholly of nerve-fibrils; they may be described as cuticular outgrowths from the sensory layer projecting into the granule-cells lying in contact with it. The cuticular outgrowths appear to rise from that layer of the sensory cells which lies just within the external limiting membrane, while from the crowd of undifferentiated sensory cells in the deeper layers (lying nearer the centre of the eye) fine nerve-fibrils descend from all sides and run out along (? within) the supporting cuticular rods prepared for them. This will explain the fibrous character of the protoplasm ascending from each rod and surrounding its own special nucleus, which can be clearly seen under the microscope in sections of the retina of the frog. It might also be associated with the longitudinal striation which has long been attributed to these structures.

From all that has been said above as to the connexion between the granules in the wandering-cells and integumentary protective structures, the development of cuticular rods is not surprising even in such a place. We have but to assume that a certain number of granules succeed in forcing their way into the outer layer of cells in the opposing sensory tissue-layer, and that these cells work them up into protective structures. The structures take the form of rods projecting into and still further impeding the advancing stream of the granules.

Microscopic evidence can be adduced which leaves little doubt that the pigment-granules do actually yield at least some portion of the material out of which the rods are built up. If this is indeed the case, it would go far towards establishing the theory here set out, that the granules endeavour to force their way forward towards the source of light and into the opposing layer, which layer, being composed mainly of sensory cells, is in consequence stimulated.

In the highest vertebrate eyes these cuticular rods may be of great length, forcing the granule-bearing cells back from the external limiting membrane, while, again, the great thickness of the retinal tissue necessitates considerable differentiation of its elements for support and, perhaps, on the one hand, for nourishment, and on the other for the removal of waste.

The Choroidal Epithelium.—Having thus briefly sketched the opposing sensory tissue, we turn to the layer of cells containing the granules which seek to reach the surface of the body whenever stimulated by light. The bodies of these cells are forced back from the external membrane of the sensory layer by the cuticular outgrowths just described, but they remain attached to it by fine protoplasmic processes. These protoplasmic strands thus run up among the cuticular rods; or, to describe it in another way, just as the granule-bearing cells, on being arrested by dense epidermal tissue on their way to the surface of other parts of the body, penetrate as far as they can between the cells composing this tissue by means of pseudopodia, so here the pigment-bearing cells penetrate with their pseudopodia between the rods protecting the retina until they are stopped by its limiting membrane. In the case of the eye for certain, and from the darkening of the skin by exposure to sunlight probably in this case also, the granules are stimulated to escape along these pseudopodia by the action of light. In the case of the eye very few apparently succeed in getting away at the tips of these cell-processes through the membrana limitans externa, and, baffled, they have to return to the cells in which they are imprisoned. In the case of the skin, however, their escape in considerable numbers into its outer cell-layers seems not only probable in itself, being quite in accordance with what the microscopic study of skins teaches us, but seems also to be required by the dark colour familiar to us under the name of sun-burning, which persists for some days, or even weeks, after the exposure has ceased *.

* Dark people, as a rule, burn darkest; in fair people the granules invading the skin are apparently not coloured, but local immigrations of coloured granules, perhaps from blood-vessels, give rise to freckles. If

Returning to the eye, the granules may be described as advancing and retreating according as they are stimulated by light or as the stimulus is withdrawn. It may also be that, like the kindred chromatophores of the skin of animals endowed with the chromatic function, they are susceptible to nerve-stimulation, inasmuch as it is said that the granules advance in a darkened eye if the companion eye is stimulated by light. But this "sympathetic" advance might perhaps be explained in another way.

While the advance is apparently due to the stimulus of the light, the retreat may be due to lateral pressure on the part of the cuticular rods. That such a pressure exists we may perhaps conclude from the fusiform shape assumed by those granules which, being on the outer portions of the cells, slide up and down most frequently between the rods. The pointed ends of these fusiform bodies lead one at first naturally to see in them the instruments for stimulating the nerves. It has been pointed out that they might, for all we know, vibrate as rapidly as cilia. It was long before I became convinced that this shape was chiefly useful in enabling the granules to force their way up and down rapidly between the closely packed rods, and also in enabling them to form compact masses, the fresh arrivals wedging themselves in between those in front. The pointed ends have, I am convinced, no other function than that of facilitating their alternate advancing and retreating movements, for rapid crowding at special points and equally rapid dispersal.

The actual cause of Light Sensation.—At first sight it must appear that no theory can be simple which seeks to explain how the eye can accurately register (as it does, say, in the process of reading) several hundreds of distinct words, each composed of many letters, per minute, each letter forming an image which remains but the fraction of a second. My theory, however, claims to be, comparatively speaking, a simple one. It assumes the existence of no forces or substances which we do not know to exist, not only in the body, but even in the eye itself; and it is, moreover, applicable to every eye, known for certain to be such, in the animal kingdom.

Just as the play of colour in the skins of animals endowed with the chromatic function is due to the constant shifting of the variously coloured granules within the chromatophores, so

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these granules really contain excretory matter which should be discharged at the surface of the body, we should be justified in concluding that the exposure of the skin to light must be generally beneficial to health.

the rapid changes in our sensation of sight are, I believe, due to slight shiftings, in obedience to the changing play of the light, of the granules between the highly sensitive rods of the retina. The distances through which the granules have to move individually can be shown to be infinitesimal. This fact is of importance, because one of the difficulties against any such hypothesis has been stated to be the great distance the granules would have to travel from the pigment-cells all the way up between the rods, and the consequent slowness of the reaction, which we know from experience to be practically instantaneous. Closer inspection shows that this difficulty does not exist. No eye is fit for vision in which the granules are contracted into the body of the pigment-cells, as any one may prove for himself who suddenly opens the shutters of a really dark room in which he has passed the night. The eye, indeed, has to be prepared for, or, in other words, to "get accustomed to," the light. The general sensation of light must precede the sensation of any distinct image, and this general sensation is brought about by the pressing forward of the granules between the sensitive rods. Before we have any distinct vision, therefore, the granules are already in position, actually causing the general sensation, Not until this is the case are we conscious of any definite images.

Leaving colour-sensation for the moment out of the question, these definite images are really only variations in the intensity of the light. These will be felt in the following way. Where a bright light falls, more granules push forward from the back; where a shadow falls, the push from behind is relieved. The movements of the individual granules in order to effect these changes of pressure need only be infinitesimal. In a crowded gangway it is often difficult to see, by any actual movement, who is pushing and who is not. We all, however, feel instantaneously both when the pressure is put on and when it is taken off. No one who has watched the movements of minute organisms under the microscope can doubt that they would supply us with far greater rapidity than that required by this theory, for the instantaneous application or withdrawal of pressure, the distances to be traversed being, as already stated, infinitesimal.

We may, then, describe our ordinary vision (apart from colour) as due to constantly varying degrees of relief from, or increase in intensity in, the general sensation of light which, during all vision, floods the eye, this general sensation being caused by the granules pressing forward between the rods and cones, and varying in numbers according to the brilliance of the light. Every shadow, every shade of a shadow, every dark moving object, every black line of the book we are reading represents so many reliefs, so many degrees, so many shiftings, and so many durations of relief from the pressure which the granules are exerting laterally upon the sensory nerve-fibrils in some way incorporated with the retinal rods.

Colour-Sensation.—No theory of colour-sensation can be satisfactory unless it can be shown to be a natural development—that is, a development, without sudden break or sudden addition of new factors, of ordinary light-sensation. It is satisfactory, therefore, to find that colour-sensation almost naturally follows from the foregoing description of general light-sensation.

That there exists some connexion between the granules and the formation of the cuticular rods is not only probable itself, but can even, I believe, be demonstrated under the microscope. We need not now discuss the details: it is enough for our purpose if this cuticular structure, the rod, varies slightly in texture in such a way as to be almost glassy near the external limiting membrane, and from this point to consist of zones in which corpuscles of increasing size (though always microscopic) are suspended. That the rod has some definite texture tending to cause it to break transversely into short lengths, histologists are agreed. We are further justified in assuming some heterogeneity in order to avoid the total internal reflection of the light down to its tip, which would take place if the rod were a homogeneous glassy structure. In addition to this specialization into zones, with different-sized corpuscles suspended in the substance of the rods, we have only to assume that, of the sensory nerve-fibrils embodied in each rod, one or more terminate among the finest corpuscles, one or more among the next coarser, and so on to the tip, where the coarsest are found. Colour-sensation would, it seems to me, naturally result from such an arrangement. We require no more movement among the pigment-granules than we required for the appreciation of the ordinary variations in light and shade. The red rays, according to the law illustrated daily in the sky, passing through all zones containing the smaller corpuscles, would be caught and dispersed on all sides by the largest granules at the tips of the rods. The pressure of the granules already crowded in the "gangways" would be immediately directed both from above and below to the point where the red light is breaking in from the side. Again, rays of shorter wave-lengths would be caught by the smaller suspended corpuscles and scattered laterally among the crowds higher up the gangways between the rods, when the pressure would at once be increased in the region of these smaller corpuscles by infinitesimal movements of the pigment-granules from both directions. In this way it would be possible to have rods dispersing laterally each colour of the solar spectrum in succession, beginning from the top with the violet. How many different zones there actually are in the longest tapering rods (" cones ") in the human eye can only perhaps be ascertained by a careful analysis of our sensations. It was long ago shown (Young-Helmholtz theory) that three elementary sensations—red, green, and violet—would be sufficient to explain the rest; but, according to our theory, there appears to be no reason why there might not be more.

According to this theory white and black would not be colours, but merely stimulation or absence of stimulation of the rods as wholes.

The curious phenomenon of colour-blindness in individuals, and perhaps also the assumed existence of racial deficiencies in the matter of colour-sensation *, might be explained as due to a failure to develop the necessary specialized gradations in the sizes of the corpuscles suspended in and composing the retinal rods. It is, on the other hand, possible that we have not ourselves reached the limit of perfection attainable in this direction.

It may perhaps be added that, while the active force causing the stimulation of the nerve-endings for the different colours would in all cases be the same, namely pressure on the sides of the rod by the crowded granules in the gangways, the actual stimulus on the nerve-fibrils would be different for each colour—in one zone of the rod the nerve-ends would be nipped between larger, in another zone between smaller, corpuscles, which also might perhaps differ in shape.

We have, then, briefly traced a theory of light-sensation and of vision which embraces all known eyes, from the simplest to the most complex, and which accounts for the most perplexing phenomena by an appeal to known factors alone. But, however connected and plausible a theory may be, the question of most importance always is, can it be proved? Is it anything more than a mere working hypothesis? While admitting that this theory is, and may perhaps long remain, only a working hypothesis, I think that it is something more. A great part of it, dealing with the elemen-

* The ancient Greeks, judging from the very limited colour vocabulary of their poets, are thought not to have been so specialized in this respect as we are to-day.

tary stages in the development of the sense of vision, is capable of actual demonstration, and on this solid foundation the rest is built. The truth of this most important "rest," which includes the phenomena of clear vision such as we know it, can only perhaps be finally established by degrees. Facts are, however, not wanting which make me believe that a rigid demonstration of it is not far off.

I will point first of all to those observations which tend to show that, in cases of frogs killed after their eyes had been exposed to different coloured lights, the pigment is found massed in a manner not unlike that in which, according to this theory, it should be massed. A chromatic scale, somewhat like that which I have sketched theoretically, is actually claimed to exist. The red light is found to mass the pigment round the tips of the rods, and so on in regular order upward. It is hardly to be expected that the records of actual discoveries in connexion with this chromatic scale would tally exactly with the requirements of the theory. The extreme mobility of the pigmented granules would render their persistence in any position, after the conditions which induced it were changed, highly improbable. It is, in fact, a matter of surprise to me that they show as much of the theoretical chromatic scale as they are said to do *.

Again, evidence in favour of the theory, to some minds perhaps of even greater weight than that already adduced, may be found in the fact that it enables us to explain such collateral phenomena as irradiation, contrasts, after-images.

Irradiation would be due to the increase in size of any bundle of strongly illuminated rods owing to the great crush and continued pressure of granules into the gangways between them. This increase in size of the area occupied by the illuminated rods would press upon the adjacent rods all round for a short distance, the pressure being soon neutralized by the emptying of the gangways (by the squeezing out of the granules) between these adjacent rods.

On the withdrawal of the light the crush in the gangways, if it has been very great owing to the brilliancy of the illumination, takes some time to relieve, during which time we have a positive after-image. As soon as it is sufficiently relieved, the granules which had been forcibly squeezed out from between the adjoining gangways force their way back again, and in doing so seem to assist in squeezing the recently congested passages empty. The positive after-image then changes, as in a moment, into a negative after-image with a

* *Cf.* Angellucci, Molleschott's 'Untersuchungen,' xiv. 1890, p. 231.

corona. Only slowly is the state of equilibrium reached; we apparently have, indeed, a veritable "oscillation" of pressure, alternately within the originally stimulated area and the region immediately surrounding it.

If, again, the congestion in the gangways between the rods of an illuminated area is not equally distributed throughout their whole length, but is localized, say, at their distal ends, which is, according to the theory, the result when the illuminating rays are red, the pressure on the surrounding region will be different. It will not affect the whole length of the adjacent rods, but only their distal ends. The pressure exerted on the distal ends of adjacent rods will squeeze the granules which were arranged here both up and down. It is probable that more will be squeezed up than down, as the downward attraction of the red rays would tend to relieve the pressure at the upper ends of the rods in the illuminated area, and render this the direction of least resistance within the gangways of the adjoining rods. While, then, the red light is massing the granules *between* the distal ends of the rods in the illuminated area, the pressure caused by these localized assemblages of granules leads to a slight massing of granules *above* the distal ends of the rods in the surrounding region. Here it should give rise to a different colour-sensation from red. Indeed, it is a necessary corollary of the theory of colour-sensation here proposed that the irradiation from any coloured image must be of a different colour. Daily experience shows this to be actually the case. According to this theory, then, the difficult phenomena known as "colour-contrasts" have hardly to be accounted for; they take a natural and necessary place in the scheme *.

One more point in evidence as to the truth of this theory. It is true that it is again indirect evidence, but its weight cannot be ignored. There has never yet, so far as I know, been any satisfactory explanation of the curious deception presented by what are known as Zöllner's parallels. If, however, irradiation is due to a real mechanical pressure, the apparent divergence of these lines admits of very simple explanation.

We may therefore briefly describe the development of visual organs in the animal kingdom as follows:—

Under the influence of light certain organisms travelling toward the light seek either to leave the Metazoan body altogether or else to discharge their contents at the surface. Such

* The whiter edge of a white image surrounded by a black border is usually also classed under the head of contrasts; but this admits of a very different interpretation.

emigration cannot take place without the cognizance of the nervous system, and where it is most pronounced, *i. e.* in the most frequently illuminated parts of the body, complications arise between the fugitives and the other tissues, notably the peripheral nerves. My suggestion is that out of these complications all the known eyes of the animal kingdom, the most complicated as well as the most simple, have in one way or another arisen.

If this theory can be established, a fascinating field of investigation will be opened out to zoologists. If such specialized structures as eyes have arisen simply by the crowding to excess of pigmented granules in the most frequently illuminated parts of the integument, may not other less specialized integumentary structures in the animal kingdom be also explained by variations in the numbers of the granules received by their formative cells? Leaving out of account the circulatory system, the tissues among which the wandering-cells have to travel towards the surface are not all equally dense, and even if soft may for one reason or another be impenetrable. Hence the migrating swarms of wandering-cells would tend to divide up into streams which would reach the surface as such, causing cuticular thickenings or prominences at such spots. We might expect to find specializations of the integumentary cuticular formations showing some slight correspondence with the sizes and importance of these streams. In investigating the movements of wandering-cells, which, avoiding the canal-system supplied by the blood-vessels, may be described as travelling across country, gravitation and the active movements of the body, as well as light, must certainly be taken into account. It is not improbable that a slowly cumulative selective action is taking place, those cells containing the most deeply pigmented granules better overcoming the attraction of the earth under the light-stimulus than those carrying less- or non-pigmented granules.

In the fuller treatise containing a detailed account of the evidence, direct and indirect, on which this theory is based, I propose to give simple diagrams to illustrate more fully the explanations, here thus briefly sketched, of colour-sensation, irradiation, colour-contrasts, and other kindred phenomena. I propose also to include an account of some of the subjective phenomena, attention to which first drew me on to seek an explanation of vision in general.

Streatham, S.W.,
January 10, 1896.